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First capture of a coelacanth, *Latimeria chalumnae* (Pisces, Latimeriidae), off Mozambique

On 11 August 1991 a large female coelacanth, *Latimeria chalumnae*, was caught off the coast of central Mozambique. We report on the capture of this second specimen from the African mainland and discuss the significance of the finding.

The coelacanths (Actinistia) have a fossil record extending back about 380 million years to the Middle Devonian with at least 121 extinct taxa.[1] The group was thought to have died out during the Cretaceous extinction as the fossil record ends about 65 million years ago. The capture of a living coelacanth, *Latimeria chalumnae*, off the south-east coast of South Africa in December 1938[2] revealed that at least one representative of this ancient group had survived into modern times. Smith's[3] prediction that the coelacanth inhabits deep, rocky reefs in tropical waters was confirmed when a second coelacanth was captured by a handline fisherman off Anjouan Island in the Comoros archipelago, western Indian Ocean, in 1952.[4] Since then, at least 172 coelacanths have been caught off the islands of Grand Comoro and Anjouan by handline fishermen[5,6] but no further specimens from the African coast have come to the attention of scientists.

In the early 1940s the Sea Fisheries Research Institute vessel *Africana I* trawled repeatedly on the continental shelf along the coast near East London, but no coelacanths were caught.[7] In 1950 a research vessel from the National Institute of Oceanography in England also searched for coelacanths off the East London coast without success. A recent search for coelacanths to depths of 370 m off the Chalumna coast of South Africa, using a manned submersible, indicated that the habitat is not entirely unsuitable, but did not locate any coelacanths.[8] The East London coelacanth may therefore have been a stray.[3]

Although the J.L.B. Smith Institute of Ichthyology has occasionally received information on coelacanths reputedly sighted off the coasts of South Africa, Kenya and Mozambique, none of these records has been confirmed.[9,10]

Capture of a coelacanth off Mozambique

On 11 August 1991 a large adult female coelacanth (Fig. 1) was caught off the coast of central Mozambique by a 29-m-long side trawler *Vega 13* (Fig. 2) belonging to a Mozambique/Japan joint venture fishing company called EFRIPEL. The trawl was shot at 15:15 and recovered at 19:00 and captured fish at depths of 40 to 44 m over a sandy bottom. The capture locality was given by the captain, Kenji Yoshida, as 17°19′S, 38°38′E, about 24 km offshore of the small port of Pebane, north-east of Quelimane in central Mozambique (Fig. 3). The site of capture is 5°37′ south of Moroni on Grand Comoro, where most coelacanths have been caught,[5] a straight-line distance of about 1 190 km across the Mozambique Channel. The capture site is about 15 km from the adjacent continental slope, which drops off steeply into deeper water (soundings of about 85 m and 1 000 m are separated by a distance of 5.5 km).

The captain of the trawler recognized the catch, which was still alive on capture, as a coelacanth and, appreciating the value of the specimen, immediately placed it in the onboard deepfreeze. The fish remained in the ship's freezer until 18 December 1991, when the trawler reached Maputo and the specimen was placed in the deepfreeze of the Department of Fisheries, Ministry of Industries, in the harbour at Maputo.

On 18 December 1991, the director of the National Museum of Natural History in Maputo, Dr A.J.P. Cabral, was notified of the capture. He collected the specimen on 19 December 1991 but did not have the preservatives or deepfreeze space to preserve it intact. He therefore instructed his assistant, Augustinho Chivindze, to skin the specimen on 19 December 1991. Unfortunately, the internal organs, musculature and notochord were discarded. The skin was dry-salted with sodium chloride for five days and then soaked in a solution of sodium chloride and aluminum sulphate. A dry mount of the specimen will be made for display in the National Museum of Natural History, formerly known as the Museu Alvaro de Castro, in Maputo.

The adult specimen measured 179 cm total length and weighed 98 kg, the heaviest coelacanth known.[5,11] Other dimensions are given in Table 1. The specimen was noted to have a very extended ventrum and, on dissection, was found to contain 26 juveniles in an advanced stage of development (Fig. 4). The juveniles were arranged in the oviduct facing towards the vent, but their exact juxtaposition was not recorded. Immediately after they had been discovered on 19 December 1991, the juveniles were placed intact in a deepfreeze at the Natural History Museum in Maputo. They range in length from 308 to 358 mm and weigh between 410 and 502 g wet weight. All the juveniles have resorbed their yolksacs, some completely, whereas in others an elongate, dark scar is still visible. The juveniles were coated with green matter which may have been derived from egg debris and/or faeces. Their scales, teeth, eyes and alimentary canal are apparently fully formed and their lateral line is prominent. A detailed description of the juveniles is in preparation.

On 24 January 1992 the three authors met at the Natural History Museum in Maputo and decided that it would be unsafe to leave all 26 juvenile specimens in the deepfreeze in Maputo. It was decided that 10 frozen juveniles should be taken to the Max-Planck-Institut für Verhaltensphysiologie in Seewiesen and 10 to the J.L.B. Smith Institute of Ichthyology in Grahamstown, with six remaining in Maputo where they

Fig. 1. The large female coelacanth caught off the coast of Mozambique on 11 August 1991. The specimen measured 179 cm total length, weighed 98 kg and contained 26 unborn young.

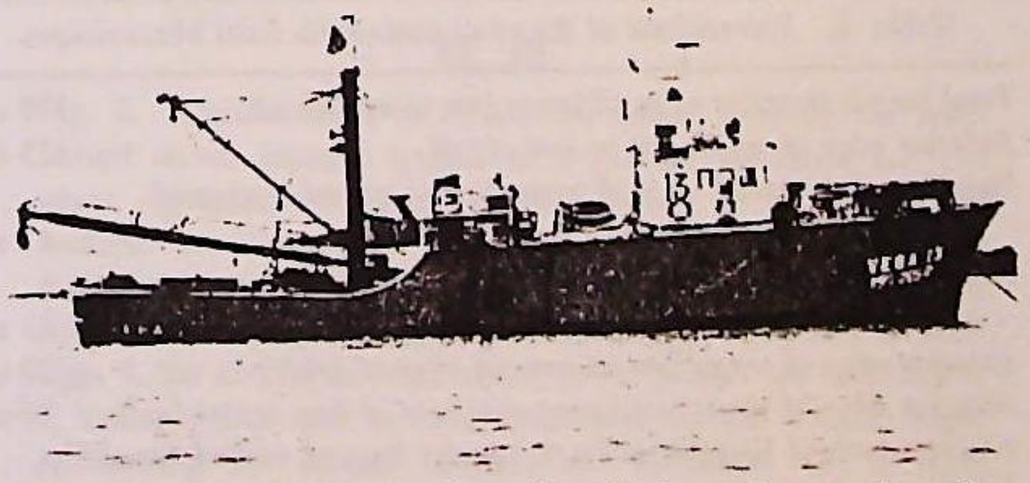

Fig. 2. The side trawler *Vega 13*, which caught a coelacanth off central Mozambique on 11 August 1991.

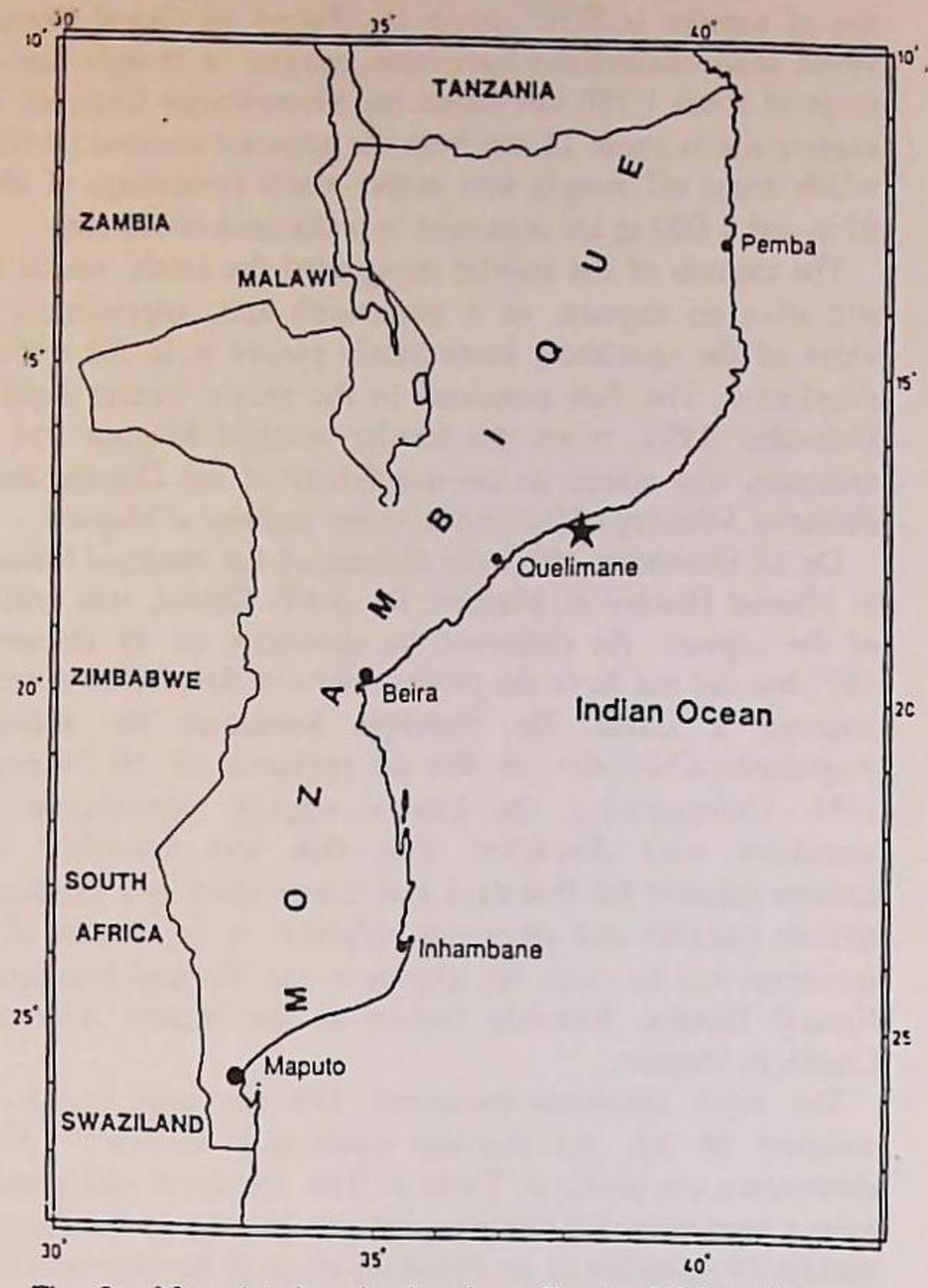

Fig. 3. Map showing the location off central Mozambique at which the adult female coelacanth was caught on 11 August 1991.

would be preserved in formalin. These arrangements were carried out on 26–27 January 1992. The juveniles in Seewiesen and Grahamstown will be curated on behalf of the National Museum of Natural History in Maputo and for the benefit of coelacanth researchers worldwide. This is in accordance with the objectives of the Coelacanth Conservation Council,[7,12] one of which is 'to promote and coordinate research on coelacanths, both living and fossil'.

Significance of the Mozambique coelacanth

The Mozambique coelacanth is only the second to be recorded from the coast of Africa and only the second, with the 1938 East London specimen, to be caught in a trawl net.[5] The presence of a large adult coelacanth on the wide, sandy continental shelf off Quelimane in central Mozambique is surprising as their preferred habitat in the Comoros is steep, rocky shores with caves and overhangs at depths from 180 to 250 m.[13] The Mozambique specimen could, however, be a stray that was

Table 1. Dimensions of the adult coelacanth from Mozambique.

Total length (anterior edge of lower jaw to end of tail)	179 cm
Anterior edge of upper jaw to end of tail	175 cm
Head length (anterior edge of upper jaw to posterior edge of operculum)	47 cm
Anterior edge of upper jaw to posterior edge of skull in dorsal midline	33 cm
Anterior edge of upper jaw to anterior edge of orbit	20 cm
Anterior edge of lower jaw to anterior base of first dorsal fin	74 cm
Anterior base of first dorsal fin to anterior base of second dorsal fin	44 cm
Total wet weight of adult	98 kg
Total wet weight of all juveniles	~12 kg

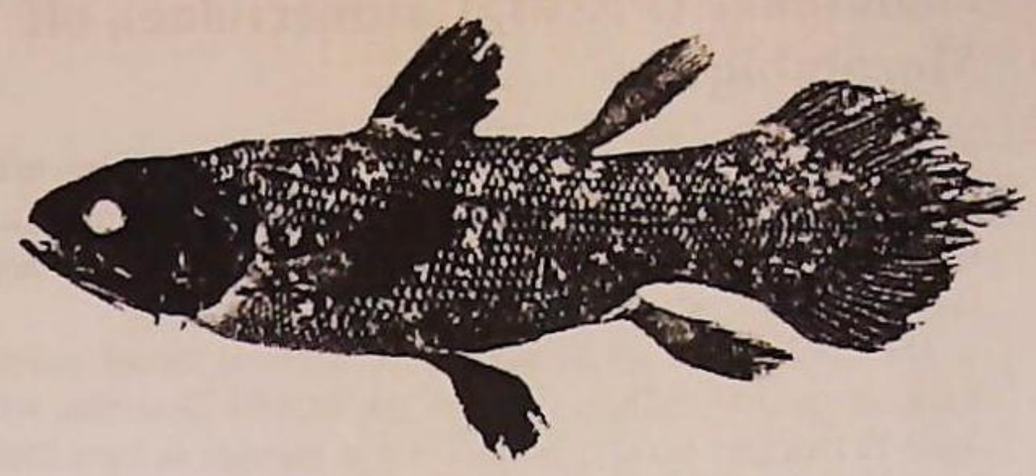

Fig. 4. One of the unborn juvenile coelacanths removed from the adult female caught off Mozambique on 11 August 1991. This specimen measured 348 mm total length. Photograph by R.E. Stobbs.

carried from the Comoros on the south-flowing Mozambique current. Research on the respiratory capacity of coelacanth adults[14] and young (G.M. Hughes, pers. commun.) indicates that they have a very low gill area ratio and would probably have difficulty absorbing sufficient oxygen from warm tropical waters.

The Mozambique coelacanth is the heaviest specimen known, exceeding the 180-cm, 95-kg female caught off Grand Comoro in 1960, and confirms the trend that all adults of more than 165 cm tend to be females.[11] The investment by the parent, as measured by the weight of the brood, is high (about 12 kg, 12% of the adult weight). The juveniles were proportionately the same size (18.4–20% of the adult length) as the five yolksac juveniles from the adult female caught off Anjouan Island in 1962 [Coelacanth Conservation Council (CCC) nos. 29.1 to 29.5, 18.9–20.4%].[5,15]

The brood size of 26 is more than five times the number of yolksac juveniles recorded in the only previous specimen (CCC no. 29) known to contain hatched yolksac juveniles,[5] and suggests that the fecundity and possibly the breeding rate of coelacanths may be higher than previously estimated.[11] The number of eggs found in gravid coelacanths ranges from 19 (CCC no. 79, 163 cm TL),[5] about 30 (CCC no. 146, 161 cm),[5] 59 (CCC no. 154, 168 cm, E.K. Balon, pers. commun.) to 67 (CCC no. 159, 164 cm, pers. obs.), which suggests that not all the eggs are fertilized or develop into juveniles. Oophagy of egg debris may occur.[16–18] Furthermore, increased vascularization of the oviduct at the site of juxtaposition with the yolksac wall is an indication that nutrient transfer may occur between the parent and the juvenile.[18] Further information on the fecundity of the coelacanth is urgently needed in order to refine the demographic model proposed by Bruton and Armstrong.[11]

Analyses are currently being conducted on the DNA of coelacanths from the Comoros and Mozambique to determine whether they are genetically distinct populations. Further efforts now need to be made, indirectly by monitoring native fisheries and directly using manned or unmanned submersibles, to establish whether further coelacanths occur off the African coast.

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The feeding niche of an extinct springbok, *Antidorcas bondi* (Antelopini, Bovidae), and its palaeoenvironmental meaning

The only antilopine species found today in southern Africa is the springbok, *Atitidorcas marsupialis*. However, a close relative, *A. bondi*, was abundant and widespread during the Late Pleistocene (Fig. 1). This animal died out at the beginning of the Holocene, *ca.* 7 000 years ago.[1] In a recent study of the Florisbad fossil mammals,[2] it was proposed that the extinct springbok was an exclusive grazer on the basis of its specialized dental features, in contrast to the modern springbok, which is a mixed feeder.[3,4] We provide evidence in support of this hypothesis from stable carbon isotopic analysis of fossil and modern springbok teeth. The results are also in accordance with the interpretation that *A. bondi* coexisted with a wide range of larger-bodied grazing ungulates[2] in a system similar to the grazing succession described for the Serengeti in East Africa.[5]

Although closely related to the extant springbok and only slightly smaller in size, the dentition of *A. bondi* is characterized by extreme hypsodonty and related wear-resistant features[2,6] (Fig. 2). Vrba[6] interpreted the differences in dental morphology between the modern springbok and *A. bondi* as alternative adaptations to a mixed diet of rough grass and shrub. The extant springbok is not a specialist grazer and can easily modify its feeding behaviour according to the condition of the veld and shift to dicotoledonous material when grass

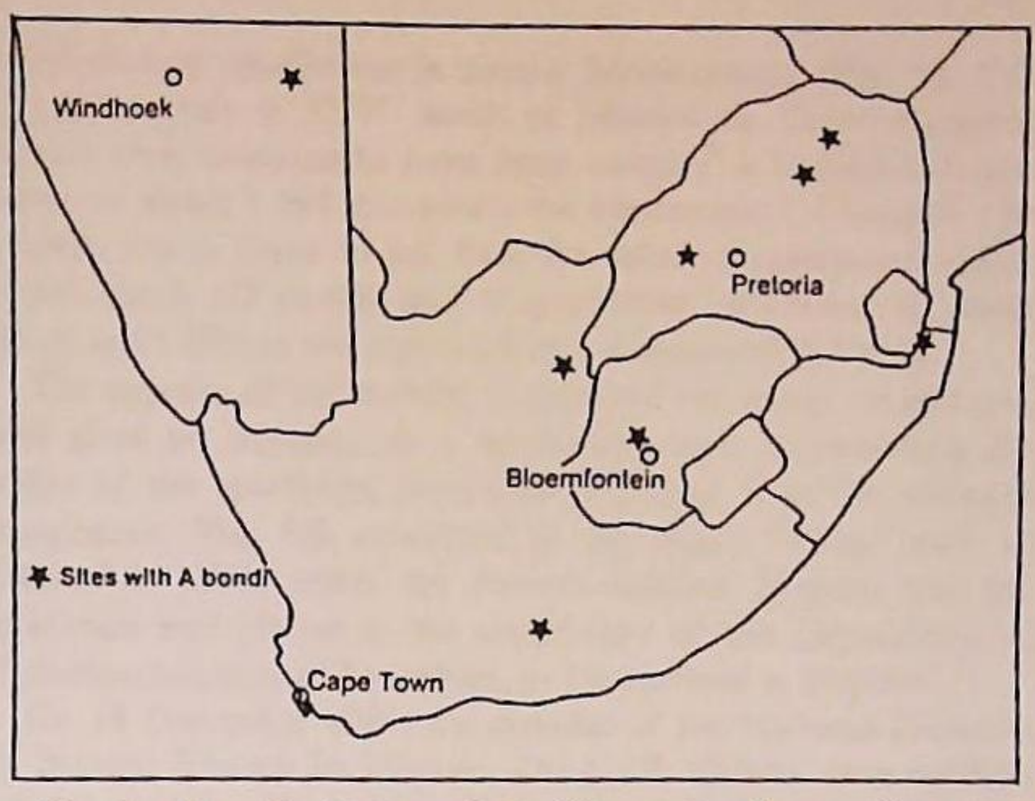

Fig. 1. The distribution of *Antidorcas bondi* according to finds from Late Pleistocene and early Holocene sites in southern Africa.

becomes unpalatable or unavailable.[3,4] This is clearly reflected in the teeth of *A. marstupialis*, which are not very high-crowned with relatively thin enamel walls, and occlusal surfaces which tend to be slightly concave. In sharp contrast to this are the wear-resistant dental features of the extinct Bond's springbok. Since attrition in ungulate cheek teeth is due mainly to dental contact and occlusal pressure and not so much the result of the initial coarseness of food,[7] only a fibre-rich diet, such as grass, which requires long periods of high intensity

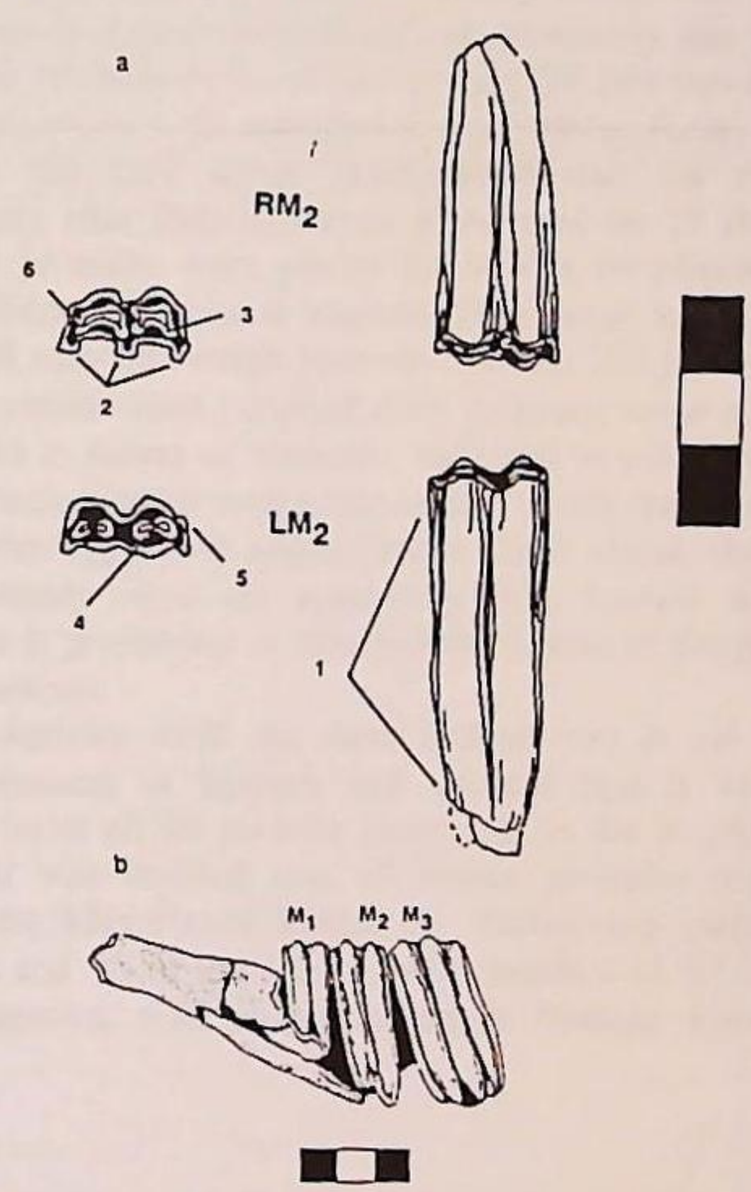

Fig. 2. The dentition of *Antidorcas bondi*, showing the specialized dental features typical of a grazing ruminant. (*a*) The upper right and lower left second molars of *A. bondi*. The features are: 1, molars are extremely hypsodont; 2, upper molars have prominent styles; 3, the enamel walls of the central cavaties of the upper molars show complicated foldings; 4, the central cavaties of the lower molars are constricted; 5, lower molars tend to have goat folds; 6, the enamel ridges surrounding the central cavaties are thickened. (*b*) A right mandible showing the dominant position of molars in the jaw, another typical feature of grazing ruminants. Scales are in centimetres.

This result can be contrasted with similar tests for the UK system, where the lag was 16 years and the distribution was positively skewed, with the peak effects at 12 to 16 lags. This suggests that whereas the UK system includes a high proportion of basic scientific research with a long gestation period, the South African research system is dominated by short-term developmental work.[11]

In the profit function the lag distribution is represented by a knowledge stock constructed using the perpetual inventory model (PIM), which is a reasonable approximation of the 'true' lag structure. Thus, the knowledge stock (KS), with R&D entering with a one period lag, at period t is

$$KS_t = RD_{t-1} + (1-\delta)K_{t-1} \quad (6)$$

where δ is the rate of depreciation, which is set at 10%, so that 90% of the weight is on the first nine years. In this application the starting value of KS, at $t = 0$, is irrelevant by 1947, because the series begins in 1929.

Applying the same methodology to the patent count series gave a lag of 12 to 13 years and again a negatively skewed distribution. So, the patent knowledge stock is approximated in the profit function by a PIM with a depreciation rate of 8.3%, which is appropriate for a 12-year lag. The patent variable is the means of allowing for both private spillovers from abroad and for the technology provided by multinational seed, chemical and machinery companies, which may or may not be performing their research in South Africa. For the non-international private sector, very little is known about R&D. This is a handicap, but need not prevent economic analysis of the returns to R&D, since private R&D is not outside the market system, like the public expenditures. Indeed, as was noted by Griliches (1973), if agricultural inputs were supplied by a monopolist, and the input statistics took proper account of quality adjustments, technical change emanating from the private sector input industries would be fully included in the input series. Such technological changes are in the farm inputs sector, not the farm sector itself (Kislev and Peterson 1982), and would not present any difficulties. It is only to the extent that the input suppliers are monopolistic competitors and that the statistical sources fail to measure inputs in efficiency units, that allowance must be made for private R&D expenditures. However, due to these two factors, not all technical change in the input industries is correctly measured at source and there will be some spillover that is caught instead in measures of agricultural productivity. Thus, in estimating the returns to R&D, all the non-market public expenditures should be included on the cost side and some proportion of private expenditures should be added.

The lags on extension and education should be far shorter, so the same elaborate lag structures need not be imposed. The model selection criteria indicated that a single one-period lag is the appropriate specification.

Lastly, since the technology variables are interdependent, the lags structures should be jointly estimated. Thus, the model selection criteria are applied to combinations of lags for the different variables in a grid search for the model that performs best.

Calculating the rate of return to research

The internal rate of return (r) is calculated using the formula from Ito (1991)

$$\exp(r, L) = \int_0^\infty \left(\frac{\partial F}{\partial (RKS)}\right) \exp(-rt)\, dt \quad (7)$$

where L is the average lag value for R&D, which is taken to be five years. The calculation reduces to

$$re^{5r} = VMP_{RKS}$$

where the Value Marginal Product (VMP) of the research knowledge stock is the shadow price of research, in Table 2, which is 4.04. Solving (7) for r gives a value of 0.44, which is a 44% internal rate of return.

Research Letters

First authentic capture of a coelacanth, *Latimeria chalumnae* (Pisces: Latimeriidae), off Madagascar

On 5 August 1995, a 32-kg coelacanth fish, *Latimeria chalumnae* Smith, 1939 (Fig. 1), was caught in a deep-set net at a depth of 140–150 m off the village of Anakaó, south of Toliara (Tuléar) on the south-west coast of Madagascar (Fig. 2). The specimen was brought frozen to the Institut Halieutique et des Sciences Marines of the University of Toliara, where it was placed in a solution of 10% formalin. The abdominal cavity was opened by an incision along the ventral midline of the body, and the internal organs were examined. The gonad is small and the sex is not apparent. The fish is in excellent condition and shows no significant differences in external morphology from specimens that we have examined from the Comoro Islands.

Morphometric and meristic data are as follows: Total length (from tip of snout to tip of epicaudal fin lobe) 133 cm; head length 360 mm, eye diameter 45 mm. First dorsal-fin spines 8; second dorsal-fin rays 27; anal-fin rays 29; pectoral-fin rays 27; dorsal, ventral and epicaudal lobes of caudal fin each with 24 rays.

The following details pertaining to the capture of this first (authenticated) record of a coelacanth from Madagascar were gleaned from interviews with Mr Regis Robinson (Mayor of Anakaó), local fishermen and a letter from Mr Dominique Couttin, who originally purchased the coelacanth from the fisherman (ZeZe of the village Soalara) who caught it. The fish was caught in a deep-set 'shark net' 100 m long by 2 m high, with a stretched mesh size of about 36 cm. These shark nets are set in depths of 100–200 m, weighted to hang about 1 metre above the bottom and baited with small fishes to attract sharks; they are usually set at about 08:30 and retrieved 24 hours later. The coelacanth was caught off the village of Anakaó in a shark net set at a depth of about 140–150 m. Never having seen a coelacanth before, the fisherman (ZeZe) was frightened and was going to throw it back, as all unusual catches are '*fady*' (taboo), because they might be poisonous; but it was so big that he decided to take it to show the Mayor (who is an experienced fisherman). Neither the Mayor nor any of the other old, experienced fishermen had seen this species before. The fish was recognized as a coelacanth by Dominique Couttin, who lives at Réunion and visits Anakaó twice a year. Couttin purchased the coelacanth from ZeZe for 25 000 Malagasy francs (US$6) and immediately took it in his boat to Toliara, where it was placed in a freezer.

Discussion

The coelacanth was known to fishermen of the Comoro Islands long before it was 'discovered' and given its scientific name, *Latimeria chalumnae*, by J.L.B. Smith in 1939; but it is

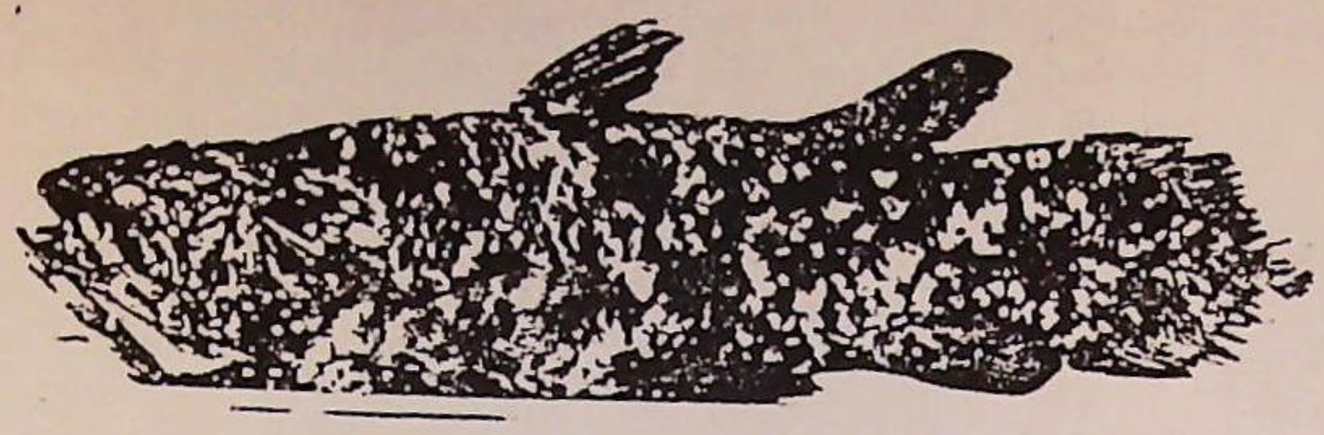

Fig. 1. *Latimeria chalumnae*, 133 cm long, mass 32 kg, from off Anakaó, Madagascar.

only recently that its behaviour and ecology have been studied *in situ* at depths of 150–400 m with the aid of research submersibles.[1] The 98-kg gravid female that was caught in August 1991 at a depth of 40–44 m off the Mozambique coast near Pebane[2] was only the second specimen known from localities other than the Comoros. Following the recognition of the Comoros as the home of the coelacanth in December 1952, at least 191 of these fishes have been caught there.[3]

At the Comoros (Grand Comoro and Anjouan), coelacanths have been observed[1,4] on steep rocky slopes with little sediment. During the day, groups were usually seen resting in caves (up to 14 fish in a cave) at depths of 150–200 m. At night the coelacanths would emerge and slowly swim or drift about near the bottom, often following gullies of old lava flows into deeper water (250–300 m, occasionally to depths of 700 m), where they appear to be searching for prey.

Anakaó is about 33 km south of Toliara, 18 km south of the Tropic of Capricorn and some 9 km south of St Augustin Bay. At a depth of 140 m, the bottom off Anakaó is mostly sand and of low relief (the shark nets are not set in rocky areas, as they would likely be snagged on the rocks and lost), and the 200-m depth contour is located about 9 km from shore.

Before 1993, sharks were regularly caught off Anakaó and in St Augustin Bay with hook and line at depths of 150–250 m. The deep-set shark nets, which were introduced some two years ago, proved to be more productive than hook and line fishing, and most fishermen have switched to this deep-netting method. Weather permitting, some 50 fishermen (usually working in two-man teams) are engaged every day in the deep-set shark net fishery off Anakaó. Since none of the local, experienced fishermen had previously seen a coelancath, it seems unlikely that a resident population of coelacanths occurs off this part of the Madagascar coast. North of Toliara, the continental shelf broadens and the 200-m depth contour is located some 20 or more kilometres from shore. This increased distance to deep water precludes most local fishermen (without motorized canoes) from deep-water fishing. For most of the west coast of Madagascar (from Morondava, at about 20°S, to the north end of Madagascar) the continental shelf extends 50–100 km offshore. This broad expanse of shallow-water habitat would prevent local fishermen from fishing at depths frequented by coelacanths; consequently, although coelacanths may occur or be resident off the west coast of Madagascar, it will require a directed exploratory fishing effort or a survey with a research submersible to find them.

Toliara is some 1300 km south of Grand Comoro, and it is feasible that a stray coelacanth was inadvertently carried off from Grand Comoro in the prevailing southerly currents that sweep round the north end of Madagascar. DNA fingerprint patterns from the pups of the Mozambique coelacanth indicated that this fish was from the same population that lives at Grand Comoro.[5]

We thank Robin Stobbs for his comments on an early draft of this paper.

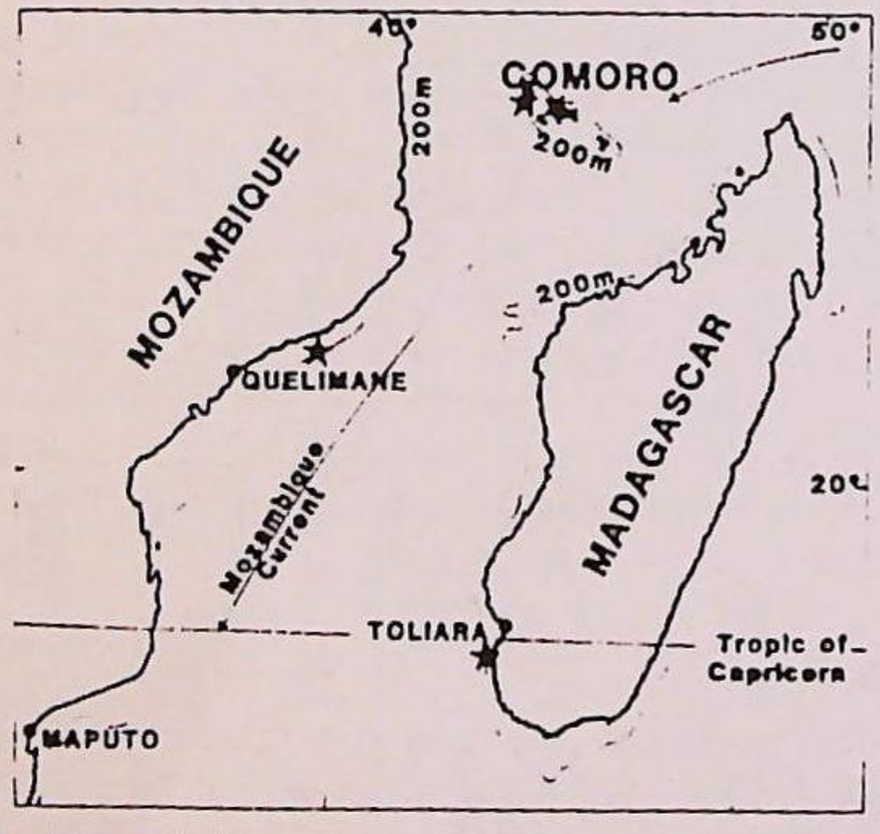

Fig. 2. Map of the Mozambique Channel showing localities of capture of coelacanths.

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